NeoBiota 25: 1–14 (2015)
doi: 10.3897/neobiota.25.8316
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Comparing functional similarity between a native and an alien slug in temperate rain forests of British Columbia

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Academic editor: *W. Nentwig* | Received 19 July 2014 | Accepted 28 November 2014 | Published 14 April 2015

Citation: Rodriguez-Cabal MA, Gibbons TC, PM, Barrios-Garcia MN, Crutsinger GM (2015) Comparing functional similarity between a native and an alien slug in temperate rain forests of British Columbia. NeoBiota 25: 1–14. doi: 10.3897/neobiota.25.8316

Abstract

The impacts of invasive alien species are greatest when they become dominant members of a community, introduce novel traits, and displace native species. Invasions by alien mollusks represent a novel context by which to compare trait differences between generalist native and introduced herbivores in terrestrial ecosystems. Here, we determined the abundance, habitat, feeding preferences, as well as the metabolic rate of the native Pacific banana slug (*Ariolimax columbianus*) and the alien black slug (*Arion rufus*) in the coastal forests of British Columbia, Canada. Through a series of observational and experimental studies, we found that alien slugs are more abundant, differ in their habitat preferences, and consumed more fungi (mushrooms) than native banana slugs. Conversely, in an enclosures experiment we found that herbivory damage by native slugs was higher compared to enclosures with alien only and control enclosures. Finally, metabolic rates were similar for both slug species. These results suggest that alien black slugs possess a suite of traits that make them functionally different from native banana slugs.

Keywords

European black slug, Gastropoda, generalist herbivores, invasive species, Pacific banana slug, metabolic rate

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Introduction

The rampant loss of biodiversity and the spread of alien invasive species are pervasive components of global change (Vitousek et al. 1997, Chapin et al. 2000, Simberloff et al. 2012), and a major priority in ecology is to understand the effects of biological invasions on native communities and ecosystems (Wardle et al. 2011, Simberloff et al. 2012). In general, the impacts of invasive species on native species are greatest when they introduce novel traits and become dominant members of a community. For example, alien herbivores can modify plant communities by directly affecting plant survival, growth and fitness through browsing, grazing and trampling (Crawley 1986, Barrios-Garcia et al. 2012) or through indirect effects by altering nutrient cycles, primary productivity, disturbance regimens, and disrupting mutualisms (Williamson 1996, Mack and D'Antonio 1998, Rodriguez-Cabal et al. 2013). Yet, it remains unclear whether alien herbivores are introducing novel traits and are, therefore, functionally different than native herbivores or whether alien herbivores are performing similarly to native herbivores, but simply have higher abundances. Moreover, while extensive research has focused on the impacts of vertebrate herbivores on ecosystems (Wardle et al. 2001, Husheer et al. 2003, Côté et al. 2004), much less is known about the mechanisms that make invertebrate herbivores successful invaders.

Invasion by alien mollusks, and slugs in particular, represents a novel context in which to compare native and introduced herbivores. Alien slugs have been identified as a global pest in a wide range of managed ecosystems, from large agricultural fields to urban backyard gardens (South 1992, Joe and Daehler 2008). In addition, slugs can play important roles in natural ecosystems and crops through their effects on seedling survival, plant fitness, vegetation biomass (Hulme 1996, Hanley 1998, Joe and Daehler 2008, Strauss et al. 2009), the facilitation of alien plant species (Sessions and Kelly 2002), the acceleration of litter decomposition (Jennings and Barkham 1979), and altering litter invertebrate populations (Ferguson 2004). Despite the potential impacts of slug invasion, little is known about whether slugs are introducing novel traits compared to native slug communities. There is limited information available for pre-invasion communities and, to our knowledge, there have been no detailed comparisons of the characteristics of native and alien slugs or their impacts on native plant communities (but see Ryser et al. 2011, Knop and Reusser 2012, Blattmann et al. 2013). Such functional comparisons are increasingly important given that native terrestrial mollusks have the highest number of documented extinctions of any major taxonomic group, most of which can be directly linked to introduced mollusk species (Lydeard et al. 2004, Nash 2004).

The Pacific banana slug (*Ariolimax columbianus*, Gould in A. Binney 1851) is a charismatic species that is native to the Pacific Northwest Region of North America, with a distribution that extends from the central coast of California through Alaska (Harper 1988). The Pacific banana slug is the second largest slug in the world (*ca* 260 mm long), lives for several years, and is the most common native slug species in coastal British Columbia (BC) forests (Gordon 1994, Forsyth 2004). Little is known about

the specific diet of banana slugs or most native slugs in BC forests (Forsyth 2004), but they are presumed to be generalist herbivores (Cates and Orians 1975) that feed upon a variety of plant species, berries (Richter 1976, Gervais et al. 1998), organic detritus and fungi (Forsyth 2004). On the other hand, *Arion rufus* L. (1758, hereafter referred to as 'black slugs') is native to western and central Europe (Forsyth 2004). Black slugs have been observed in BC since 1941 and have become the most common slug found in the southern portion of the province (Forsyth 2004). Black slugs tend to be smaller than banana slugs, growing up to ~180 mm long, but appear to be similar in their generalist diet, feeding upon animal feces, carrion, fungi, lichens and plants (Forsyth 2004). Unlike the banana slugs, black slugs live for only a single year (Hamilton and Wellington 1981). These alien slugs are also known to be aggressive towards other slugs (Forsyth 2004), though little work has been done on the impacts of the invasive slugs on BC flora or fauna, and whether they have negative effects on the abundance of Pacific banana slugs is unknown.

Despite the large size and high visibility of both banana and black slugs, little is known about the ecological importance of either species for forest ecosystems. Moreover, the ecological impacts of European black slug invasion remain unknown for coastal rain forests, despite being highly abundant in the understory (Rodriguez-Cabal pers. obs.). Here, we use observational and experimental studies to compare native Pacific banana slugs and the alien black slugs in the coastal forest of BC. Specifically, we ask whether there are differences between the banana slug and the alien black slug in (1) abundance and (2) feeding preferences. Next, we compare the metabolic rate as a key trait that might vary between native and alien slugs for two main reasons. First, we suspected that there could be potential differences in thermal tolerance between the two species as a result of differences in their coloration (yellow versus black), which, in turn, could allow for differences in foraging time. Second, we wanted to determine whether slugs have different metabolic rates that could explain any possible differences in food consumption rates between the two species. These comparisons allow us to begin to understand the general ecological role of slugs in coastal forest ecosystems and determine whether alien slugs are playing functionally similar roles as native slugs, thereby providing general insight into the effects of slug invasions.

Methods

Study site

We conducted this work between June and August of 2012 at the Malcolm Knapp Research Forest (MKRF), which is a 5,157 ha research forest in Maple Ridge, British Columbia, Canada (49°16'N, 122°34'W). The most common overstory trees in this forest are evergreen red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), and the western hemlock (*Tsuga heterophylla*). The understory is dominated by Pacific blackberry (*Rubus ursinus*), salmonberry (*Rubus spectabilis*), red Huckleberry (*Vaccini-*

um parvifolium), salal (*Gaultheria shallon*), Pacific oak fern (*Gymnocarpium dryopteris*), common sword fern (*Polystichum munitum*), as well as a diverse assemblage of lichens and bryophytes. Forest harvesting has occurred in MKRF since 1949, which has led to a range of age classes from clear cuts, second and third growth, some small patches of > 400 year old growth forest, and different combinations of overstory species.

Slug abundance

We compared banana and black slug abundances using pitfall traps at 15 sites throughout MKRF in four different types of dominant forest overstory: cedar (n = 4 sites), Douglas fir (n = 4 sites), hemlock (n = 4 sites) and clear cuts between 2-5 years old (n = 3 sites). Forest sites were selected to encompass a range of forest ages at the study site (from 60 to 200 years old) and were at least 1 ha in size. Within each site, we placed a 3 × 3 grid of pitfall traps spaced 5 m apart (total area of 100 m^2). At each point of the grid, we placed a single pitfall trap made of SOLO® Red Cups (473 mL, 9.86 cm in diameter) containing a sponge soaked with beer (typically a light Canadian-brand lager) as beer is attractive for snails and slugs (Edwards 1991). Pitfall traps were buried flush with the ground. We covered each trap with elevated wooden cover boards (25 × 25 cm). Because beer traps may attract one species more than the other, beer traps may yield biased estimates of natural slug abundance. We therefore used wooden cover boards to provide a combined estimate of slug abundance. Because the wooden boards were covering the beer traps we counted the total number of slugs using the combined methods. The use of both methods, beer traps and wooden boards, might reduce the bias of any one sampling method. After 24-hours, we counted and identified all of the slugs in the beer traps and under the cover boards. We repeated the sampling once per month (n = 3) during the summer (June to August) on days with similar weather conditions. Captured live slugs were brought back to the lab for use in cafeteria experiments (see below).

We used Generalized Linear Models (GLM) using a Poisson distribution with a log link function to compare slug abundances by habitat type (cedar, Douglas fir, hemlock and clear cuts) and slug type (native vs. alien). We calculated slug abundance as cumulative number of slugs (summing the total number of slugs captured at each site during the summer) in each environment. Our objective of slug sampling was to obtain relative estimates of their abundance over space and time, so we considered the combined use of beer traps and wooden boards sampling method as adequate for this purpose. As we removed the captured slugs in previous censuses, we were not re-sampling the same individuals.

Cafeteria experiments

A total of 189 slugs (90 native and 99 alien) were collected from MKRF to assess their feeding rates for fruits of common native understory plant species and fungal fruit-

ing bodies (i.e. mushrooms). Individual slugs were kept in separate plastic containers (33.8 cm × 21.6 cm × 11.9 cm, Rubbermaid, Inc., Huntersville, NC, USA) on a standard diet of lettuce (*Lactuca sativa*) for 72 hours prior to feeding trials. A paper towel dampened with water was placed at the bottom of the container to prevent desiccation. We then collected fruits from several plants of the four most common shrubs in the study area (Pacific blackberry, salmonberry, red Huckleberry and salal). As we had previously observed considerable slug damage to understory mushrooms at MKRF, we used another set of 35 slugs (15 natives and 20 aliens) to assess the rate of feeding on store-bought white button mushrooms (*Agaricus bisporus*) between banana and black slugs. We recorded the percent consumed of the total volume for fruits and mushrooms after 48 hours in each feeding trial (Strauss et al. 2009).

We used GLMs using a binominal distribution with a logit link function to compare the ratio of the volume of fruit and mushroom consumed over the total volume of the fruit and mushroom by native vs. alien slugs.

Field mesocosms

To measure the individual and combined impacts of native and alien slugs on forest understory plants, we established a field mesocosm experiment in a Hemlock-dominated overstory site at MKRF in July of 2012. Mesocosms consisted of 0.25 m^2 × 0.4 m enclosures cages (n = 37) in which we planted a standard density of common understory species (see below). We used native and alien slugs, as well as seedlings, collected from the study site. Cages were constructed using a pair of wooden cedar frames (0.5 m × 0.5 m × 0.2 m). We lined the bottom of one frame with window screen (to prevent slugs from escaping) and filled the cage 50% full of a standard store-bought top soil. We then transplanted a single seedling of each of the seven most common understory plants, including hemlock, cedar, Douglas fir, huckleberry, salal, *Rubus* spp., as well as a common sword fern frond. Finally, we filled 25% of the soil surfaces of the cage with moss (See S1 for photo of a mesocosm). Next, we covered the top of another wooden frame with window screen and stacked this frame on the one filled with native plants. We used duct tape to seal the seam between the two frames.

We distributed mesocosms haphazardly throughout the site in relatively flat areas free of woody shrubs. We then established experimental additions of slugs at low, medium and high slug densities, mimicking the densities of slugs observed in our pitfall trapping. Low-density treatments included 1 slug per mesocosm of either banana (n = 5) or black slugs (n = 5). Medium density treatments included 2 slugs of either banana (n = 3) or black (n = 3) slugs, as well as a mix containing one banana and one black slug (n = 3). Similarly, our high-density treatments contained 4 slugs of either banana (n = 3) or black slugs (n = 3), and a mix of two banana and two black slugs (n = 3). Finally, there were also control boxes containing no slugs (n = 9).

After 30 days, which was enough time for the slugs to consume food items in the mesocosms, we scored the slug damage on leaf. We visually assigned damage scores to

every seedling and fern frond. We scored each leaf to one of 11 damage categories based on percent leaf area removed (0, 1-5, 5-10, 10-20, 20-30…90-100%). The same observer (MARC) scored all damage to maintain consistency across samples. As there were no major differences in the response of individual plant species within plant functional groups, we combined data as tree seedlings, shrubs and ferns. Also, as we found no effect of slug density, we lumped together the different slug densities into four groups: alien (n = 11), native (n = 11), mixed (n = 6), and control (n = 9). Finally, we compared the effect of slug type (native vs. alien) and plant type on the percent leaf area removed (PLAR) using a two-way ANOVA. PLAR was log-transformed prior to analysis to improve normality and reduce heteroscedasticity. For clarity, we show the untransformed values in all figures. We used JMP Pro 10 (SAS Institute Inc., Cary, NC) for all analyses.

Metabolic rate

To compare metabolic rate between native and alien species, we collected ten banana slugs (Mean ± SD; mass = 17.34 ± 5.80 g) and ten black slugs (mass = 8.67 ± 2.14 g) from the forest and transferred them to plastic containers (see details in Cafeteria experiment section above) in the laboratory. Two slugs of the same species were housed in each holding container and fed lettuce daily. Containers were also cleaned daily. All slugs were held at room temperature (~22 °C) and at 12:12 L:D photoperiod in the lab for the entirety of the experiment (September 24th, 2012 to October 24th, 2012).

To obtain a proxy of standard metabolic rate (SMR), we monitored slug oxygen consumption following acute exposure to several temperatures. Oxygen consumption trials were conducted using air-filled 250 mL glass respirometers submerged in a temperature-controlled water bath. Oxygen consumption of both native and alien slugs was then measured at seven different temperatures: 5, 10, 15, 20, 25, 28, and 30 °C. Temperatures were maintained using a Lauda RM6 compact thermostat (Lauda-Brinkmann, LP, Delran, NJ). Prior to testing, slugs were fasted for 24 hours, weighed and placed into respirometers moistened using sterile water to avoid desiccation. Slugs were placed in unsealed respirometers at the test temperature twelve hours prior to measurement of oxygen consumption, which was measured in sealed respirometers using Neofox oxygen probes (Ocean Optics, Dunedin, FL) with a sampling rate of once every 5 seconds. Probes were calibrated every day prior to data collection. Declines in oxygen levels were monitored for 40–120 minutes (depending on temperature), and the rate of oxygen consumption was determined from the linear portion of the trace. The final oxygen level at the end of the trial was never less than 90% of normal air. Following each trial, slugs were removed from the respirometers, re-weighed, returned to holding containers, and fed a standard lettuce diet. Slugs were fed for at least one 24-hour period before being fasted and tested at subsequent temperatures. Ten different slugs were tested per day (5 native, 5 alien), and the use of two oxygen probes allowed concurrent testing of two slugs (1 native and 1 alien). We used separate linear models with body mass as a covariate to determine whether alien and native slugs had different metabolic rates.

Results

Slug abundance

Overall, we found that black slugs were ~9× more abundant than banana slugs (GLM on Poisson distribution; $\chi^2 = 263.99$, $P < 0.0001$), and there was a significant interaction between slug type and forest type (Table 1 and Fig. 1). Alien slug abundance was higher in Douglas fir (mean: 25.5 slugs/site; SD: 14.25) and clear cuts (mean: 22.67 slugs/site; SD: 8.14) compared to cedar (mean: 7.75 slugs/site; SD: 7.27) and hemlock (mean: 7.75 slugs/site; SD: 6.95; $F_{3,14} = 3.63$, $P = 0.048$) overstories. Despite that the abundance of native slugs were ~5× and ~1.5× more abundant in cedar sites (mean: 2.50 slugs/site; SD: 1) and hemlock sites (mean: 2.25 slugs/site; SD: 1.50) than in Douglas fir sites (mean: 0.50 slugs/site; SD: 0.58) and clear cuts (mean: 1.67 slugs/site; SD: 1.53), we did not find a significant difference in the abundance of native slugs across the different habitat types (Fig. 1).

Cafeteria experiments

We found no difference between slug species in the amount of fruit consumed by the slugs in our cafeteria experiment (GLM on binomial proportions; $\chi^2 = 0.01$, $P = 0.9260$). We found that both native and alien slugs preferred Pacific blackberry, salmonberry and salal over the red Huckleberry (native: $F_{3,167} = 12.69$, $P < 0.0001$; alien: $F_{3,182} = 11.83$, $P < 0.0001$). On the other hand, alien slugs consumed ~7× the amount

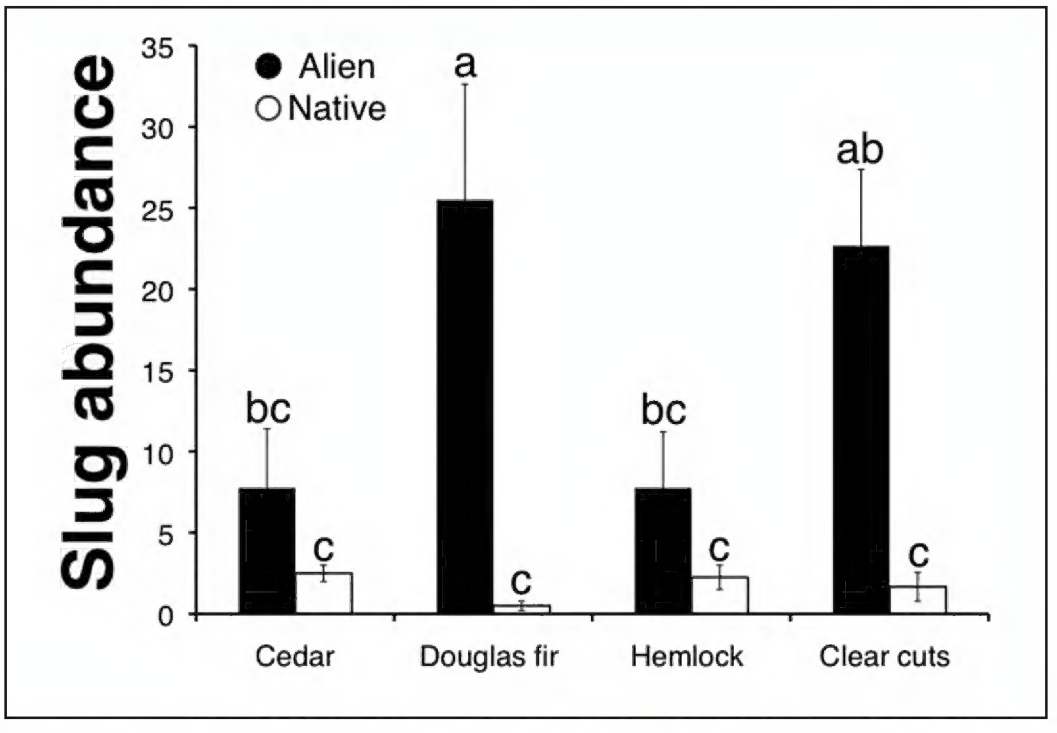

Figure 1. Alien black slugs were 50× and 14× more abundant than native banana slugs in Douglas fir and clear cuts respectively (mean ± SE, letters indicate significant differences among treatments after separate Wilcoxon test corrected with Bonferroni corrections). Taking all the sites together the alien black slug was ~9× more abundant than the banana slug ($P < 0.0001$).

Table 1. Results from a GLM examining native and alien slug abundances across different forest types, including cedar, Douglas fir, hemlock, and clear cuts. Bold values are significant at $P < 0.05$.

	Source	df	χ^2	*P*-value
Slug abundance	Model	7	263.99	**< 0.0001**
	Forest type	3	2.18	0.5362
	Slugs (native vs. alien)	1	151.46	**< 0.0001**
	Interaction	3	24.187	**< 0.0001**

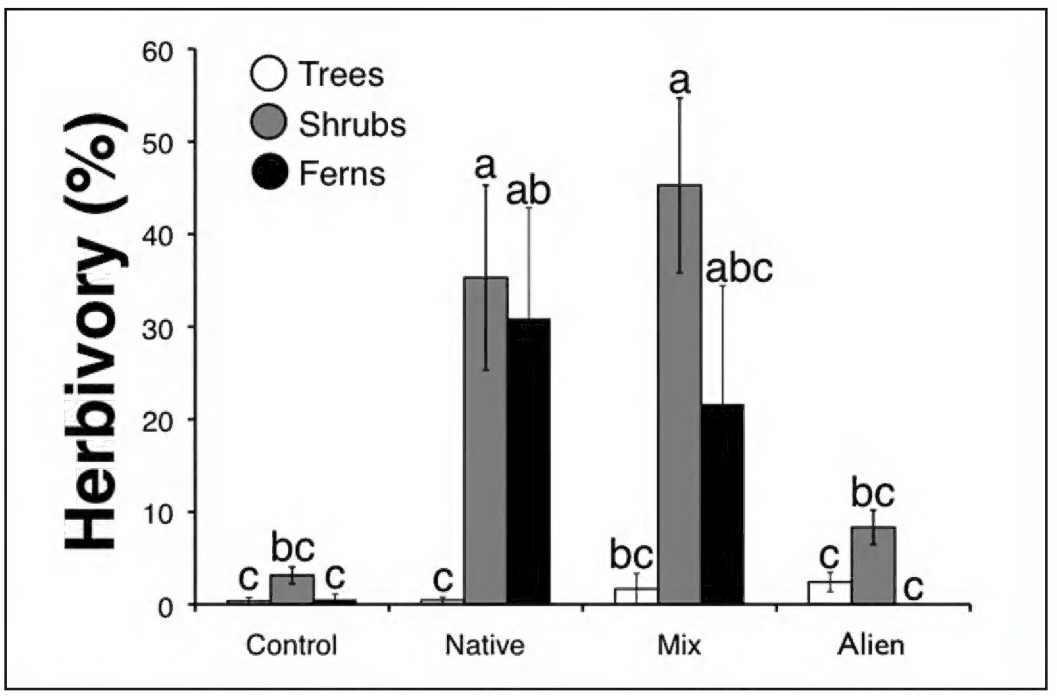

Figure 2. Herbivory was greater in banana slug and mixed enclosures than in alien and control enclosures ($P < 0.0001$), driving by greater preference of banana slugs for native shrubs and ferns compared to alien black slugs (mean ± SE, letters indicate significant differences among treatments after separate Wilcoxon test corrected with Bonferroni corrections).

of white button mushrooms compared to native slugs (GLM on binomial proportions; $\chi^2 = 14.99$, $P < 0.0001$), which was consistent with our field observations of alien slugs commonly feeding on fungi fruiting bodies (i.e. mushrooms) in the forest (see S2 photo). We did not observe native slugs feeding on forest mushrooms.

Field mesocosms

We found that herbivory was ~6× higher in native slug and mixed slug enclosures compared to alien only and control enclosures (two-way ANOVA; $F_{11,99} = 10.08$, $P < 0.0001$; Table 2). Damage rates also varied between plant functional groups, with shrubs and ferns showing the highest levels of slug herbivory and tree seedlings the lowest (Fig. 2). There was no interaction between slug type and food type (Fig. 2), driven by native slugs consuming disproportionately more shrubs and ferns than alien slugs.

Table 2. Results from a two-way ANOVA comparing slug herbivore on different plant functional groups (trees, shrubs and ferns) in experimental mesocosms. Bold values are significant at $P < 0.05$.

	Source	df	*F*	*P*-value
Slug abundance	Model	11	10.08	**< 0.0001**
	Food type	2	29.56	**< 0.0001**
	Treatment	3	10.17	**< 0.0001**
	Interaction	6	3.74	**0.0021**

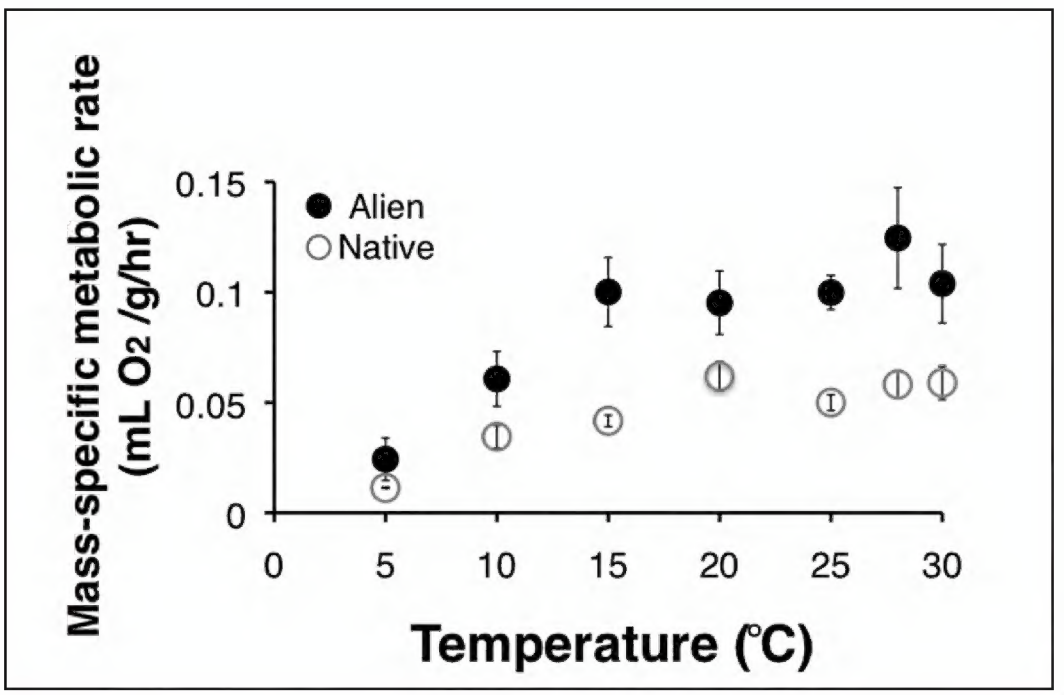

Figure 3. The effect of temperature on metabolic rate (MO_2) was similar for both native and alien slug species, but mass-specific metabolic rate was higher for the alien black slugs.

Metabolic rate

When we compared the effect of temperature on slug metabolic rate (MO_2), we found that the metabolic rates for both slug species have the same general qualitative pattern of response with change in temperature (Fig. 3). As expected based on thermodynamic considerations for ectothermic species, metabolic rate increased with temperature, but only up to approximately 15 °C, after which point it remained constant as temperature increased (Fig. 3). All slugs survived up to the highest temperature tested of 30 °C. Mass-specific metabolic rate was higher for the alien slugs than for the native slugs at all temperatures, but this difference resulted from the differences in body mass between the two groups, as the alien slugs were smaller. A linear model testing the effects of species, temperature, and body mass on MO_2 revealed a highly significant effect of body mass ($P < 0.0001$) and temperature ($P < 0.0001$) on MO_2, but no significant effect of species ($P = 0.57$). In addition, there was a significant interaction between mass and species ($P = 0.002$).

Discussion

In this study we found that alien black slugs were more abundant and consumed a greater quantity of mushrooms than native banana slugs. The fact that alien slugs are much more prevalent compared to native slugs could be explained by two mechanisms. First, alien slugs could have a direct negative effect on native banana slugs. Alternatively, alien slugs might not reach high abundance where native slugs are performing well, in which case native banana slugs could have a direct negative effect on alien slugs in cedar and hemlock forests. Because we do not have data on native slug abundance prior to the invasion of alien slugs, we cannot verify or reject either of these two possible explanations without further study. Although some studies have shown that alien slugs can outcompete native slugs (Rollo 1983), other studies have shown no effect of the alien slugs on native slugs (Hamilton and Wellington 1981).

It is possible that the higher abundances of alien slugs found in Douglas fir forests might reflect their diet preferences for fungi, as indicated in our cafeteria experiments and field observations. While this was a simple assay using store-bought white button mushrooms, Douglas fir forests depend heavily on ectomycorrhizal fungi symbiosis and can have high abundances of mushrooms. For example, the presence of the fruiting bodies of ectomycorrhizal fungi have been shown to influence the abundance of small mammals in forest stands (Carey 1995, Maser et al. 1978). Given our observations of slug damage to mushrooms at our study site, we think that fungi represent an important food source for the alien slugs and warrant further study for understanding the impacts of slug invasions on native tree and fungal communities.

The cafeteria experiment also revealed that alien and native slugs have similar preferences for fruits, particularly berries that dominate the understory in coastal BC forests. We observed intact seeds passing through native and alien slug guts, suggesting the potential for seed dispersal. In fact, previous studies have found that banana slugs consume fruits of several shrubs in these forests, decreasing the survival of salmonberry, and increasing the germination rate of large-flower fairy-bells (*Prosartes smithii*, see Gervais et al. 1998 for a complete list of species). However, no study to our knowledge has been conducted comparing the roles of native and alien slugs as seed dispersers or seed predators in this system and these interactions warrant further study.

Our results from the mesocosms indicate that neither the native nor the alien slugs appear to consume conifer tree seedlings, which is a positive result for seedling plantations and forest management [but see, Cote et al. (2005), where slugs were the most common predators of seedlings of black spruce (*Picea mariana*)]. Moreover, alien slugs did not feed upon ferns and scarcely fed upon shrub seedlings in the mesocosm experiment (Fig. 2). Therefore, it is possible that slug invasion will have the greatest impact through the consumption of fruits of many of the understory berry and fungal species in the coastal forests of BC.

When we compared the effect of temperature on slug metabolic rate (MO_2), we found no differences in the metabolic rate for both slug species. Thus, the differences in

their diet are not based on different overall metabolic rates and both species are likely active at similar temperatures in the forest. The differences in the diet of these two species of slugs could be due to variation in the reproductive cycle or the anatomy of the slugs. First, the black slug completes its somatic growth and accumulates reproductive reserves within a single year (Rollo 1983a,b), while native banana slugs live for several years (Hamilton and Wellington 1981). Thus, alien slugs might have to feed more in order to complete its annual life cycle. Second, larger body sizes tend to have higher absorption rates and so, by being smaller, it is possible that black slugs would need to feed more than larger banana slugs (Hamilton and Wellington 1981). Moreover, our results indicate the potential for both native and alien slugs to act as seed or fungal spore dispersers or predators in the temperate rainforests of BC, which has been a poorly explored role of slugs. While further experimental work is required to reveal whether alien slugs are having a negative impact on banana slugs, our results suggest that alien slugs possess different traits in addition to shorter life cycle that make them functionally different from the native banana slugs. Consequently, the results of our study warrant further research, particularly if the alien black slugs are displacing native banana slugs, as these two species are the most conspicuous slug species in the forest ecosystems of the Pacific Northwest.

Acknowledgements

We thank Ionut Aron and MKRF for facilitating our field studies and Larissa Schaub for assistance carrying out the slug metabolic rate trials.

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Supplementary material 1

Mesocosm

Authors: Mariano A. Rodriguez-Cabal, Taylor C. Gibbons, Patricia M. Schulte, M. Noelia Barrios-Garcia, Gregory M. Crutsinger

Data type: JPEG Image.

Explanation note: Detail of the mesocosm

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Supplementary material 2

Alien black slug

Authors: Mariano A. Rodriguez-Cabal, Taylor C. Gibbons, Patricia M. Schulte, M. Noelia Barrios-Garcia, Gregory M. Crutsinger

Data type: JPEG Image.

Explanation note: Alien black slug eating a mushroom in the forest.

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